

**LIFE HISTORY OF SCHISTOSOMATIUM
DOUTHITTI (CORT) ***

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Introduction.

Trematodes belonging to the family Schistosomatidae have long attracted the attention of medical men and parasitologists because three widely distributed species, *Schistosoma japonicum*, *S. haematobium* and *S. mansoni*, are parasitic in man, and in endemic regions are the cause of important human diseases. These schistosomes, with a few exceptions, have received more consideration than any other trematodes, but since none of the three forms are found in the United States and Canada the stages in their life histories have not been available to many teachers and students. The present paper touches upon all stages in the life history of a schistosome inhabiting small mammals of North America and since the intermediate hosts are widely distributed, it is probable that the parasite also may have a wide distribution. The complete life history can be maintained in the laboratory where the snail and mammal hosts can be grown for many generations, thus providing good material for the demonstration of a schistosome life history in all details and for research on various aspects of pathology, physiology, immunology and nutrition, as they relate to the host. Indeed, that the cercarial stage of this trematode was one of several species capable of producing schistosome dermatitis has already been demonstrated by Cort (1928). The present species

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is also adequate for the study of various biological problems pertaining to the parasite, to which my own work has been confined, and for the investigation of sex determination in dioecious trematodes.

Historical review.

The first digenetic trematode exhibiting sexual dimorphism was described by Rudolphi (1819) under the name *Distoma canaliculatum*. It was discovered in birds and has been renamed *Ornithobilharzia canaliculata* (Rudolphi, 1819) Odhner (1912). A second species of trematode with separate sexes was described by Bilharz (1852). These worms, which were found in the portal system of an Egyptian peasant and described as *Distoma haematobium*, have since become known as *Schistosoma haematobium* (Bilharz, 1852) Weinland (1858). Following these descriptions several other species exhibiting sexual dimorphism were described, but not until 1904 was the now well known form *Schistosoma japonicum* described by Katsurada. A few years later (1907) Sambon gave an account of a third widely distributed form, *Schistosoma mansoni*.

Looss (1899) created the family Schistosomidae* to include those trematodes which are characterized by being sexually dimorphic. In this respect they differ from all other trematodes described thus far, including the hermaphroditic bloodflukes which occur in turtles and fish, and species of the genus *Wedlia*, family Didymozoonidae, which show complete gonochorism. The members of the family Schistosomatidae are known only from the portal system of birds and mammals.

Detailed historical accounts of the early investigations on schistosomes, especially the human forms, have been given by Leiper (1915), Leiper and Atkinson (1915), Cort (1919), Manson-Bahr and Fairley (1920), and Faust and Meleney (1924). These accounts review the early descriptions of species, the experimental work on life histories, the principal features of which were the discoveries by Miyairi and Suzuki (1913-1914) of an intermediate molluscan host and the larval stages which develop in this host, and finally the completion experimentally of the life histories of *Schistosoma japonicum*, *S. haematobium* and *S. mansoni*. These schistosomes are of considerable importance in medicine as the cause of human schistosomiasis.

Information of a taxonomic nature on the schistosomes has been brought together by E. W. Price (1929). He recognized twenty-six

* Poche (1926) has pointed out that this family name is incorrectly derived from the Greek and that it should be Schistosomatidae.

species, fourteen of which occur in birds and twelve in mammals. These twenty-six species are grouped into eleven genera. For two of these species only the eggs have been described, neither male nor female being known. Besides these species there are two more whose males are unknown and four whose females are unknown.

The life histories of six species have been described, four belonging to the genus *Schistosoma*, one to the genus *Schistosomatium* and one to the genus *Bilharziella*. Miyairi and Suzuki (1913-1914) completed experimentally the life history of *Schistosoma japonicum* and Leiper (1915) worked out by the same method the life histories of *S. haematobium* and *S. mansoni*, thus establishing these forms as distinct species. Liston and Soparkar (1918) described the life history of *S. spindalis* and Tanabe (1923) gave an account of the life history of *Schistosomatium pathlocopicum*. Oiso (1927) described the life history of *Bilharziella yokogawai*. All of these species are parasitic in mammals with the exception of *B. yokogawai* which is found in birds.

The schistosomes have a world wide distribution in temperate and tropical climates, but none of the three species which have been mentioned as of importance from the medical standpoint are at present distributed on the North American continent north of Mexico. Five of the known species of schistosomes were originally described from North America. Another species, *Bilharziella polonica*, first described from birds in Europe, was reported by Price (1929) from North America. The life history of only one of the six species reported from North America, *Schistosomatium pathlocopicum*, has been completed experimentally. Tanabe (1923) collected snails of the species *Lymnaea palustris* Müller from the Back Bay Fens of Boston from which he obtained some larval schistosomes. With these cercariae he infected experimentally mice and rats, and later recovered the mature worms from the portal system of the infected animals.

A brief description of a second species of *Schistosomatium*, *S. douthitti* (Cort), was published by the writer in 1929. The present paper is a more complete account of the life history of this parasite, the seventh to be made known for this group and the second to be described in North America.

Statement of problem.

The problem chosen for this thesis consisted of three parts: (1) to complete experimentally in parasite free hosts the entire life history of a schistosome of which the cercarial stage, *Cercaria douthitti*, alone was known, (2) to study in detail the morphology of each phase in

the life history of the parasite and (3) to find the natural host of the adult worm.

Classification.

The schistosomes which are the subject of this paper differ in several respects from those described by Tanabe (1923) as *Schistosomatum pathlocopicum*, but their resemblance to the latter is such as to justify placing them in the same genus. This species then becomes *Schistosomatum douthitti* (Cort) as stated in my preliminary paper (Price, H. F., 1929). The structural details upon which this determination is based are discussed in connection with the descriptions of adult worms.

Material.

Material for the study of the various phases in the life history of *Schistosomatum douthitti* was obtained from the two kinds of hosts of this parasite, snails and small mammals, most of the material being secured from experimentally infected animals. Daughter sporocysts and cercariae were obtained from three species of naturally infected snails, *Lymnaea stagnalis* collected from Third Sister Lake near Ann Arbor, *Lymnaea palustris*, from pools at the west end of Third Sister Lake and from woodland pools a mile west of this lake, and *Physa gyrina*, from pools near the Huron river at Delhi, Michigan. Mother and daughter sporocysts and cercariae were also obtained from experimentally infected *Lymnaea stagnalis* and *Lymnaea palustris* which had been raised in the laboratory from eggs. Adult worms were secured from naturally infected meadow mice and from experimentally infected rats and mice. All of the rats and mice used as hosts were raised in the laboratory and known to be without parasites. The two types of hosts of this parasite will be considered later.

Methods of study.

Technique. Adult worms, cercariae, mother sporocysts and daughter sporocysts were studied both alive and preserved. Mature male and female worms were also studied from sectioned material. Undeveloped and developed eggs, and miracidia were studied only from living material.

Mature worms were dissected from the hepatic portal veins with fine needles and then placed in normal salt or Ringer's solution. Living worms were studied either unstained or stained intravitaly with Nile blue sulphate. Specimens to be preserved were first relaxed in cold water for ten minutes or longer and then killed in sublimate-acetic solution. These were stained with paracarmine, Mayer's alco-

holic cochineal, Ehrlich's acid haematoxylin or with stain prepared from grape skins. Living cercariae were studied unstained or after staining with *intra vitam* stains. Cercariae preserved in hot 10 per cent formalin were measured and studied while still in this fixative. Mother and daughter sporocysts were studied alive and unstained or were killed in sublimate-acetic and stained like the mature worms. Fully developed eggs and miracidia were studied only while alive, either unstained or stained intravitaly. Twenty-nine *intra vitam* stains, varying greatly in their staining properties, were tried on miracidia. These stains, unless stated otherwise, were prepared as saturated aqueous solutions, but used in considerable dilution. The *intra vitam* stains used were: alizarine red, benzopurpurin, benzo-purpurin 4B, biebrich scarlet, Bismark brown—1 per cent aqueous, brilliant cresyl blue, congo red, gentian violet, haematoxylin—5 per cent aqueous, iodine in KI, indigo-carmin, Janus green B, cresylecht violet, light green—5 per cent aqueous, malachite green, meldola blue, methyl green, methylene blue, neutral red, neutral violet, Nile blue BB, Nile blue sulphate—0.2 per cent aqueous, pyronin, rhodamine G, safranin, thionin, toluidine blue, trypan blue and trypan red.

Among these stains brilliant cresyl blue, gentian violet, Janus green B, malachite green, methylene blue, neutral red, Nile blue sulphate and thionin have been the most valuable in staining and differentiating the structures of the miracidium. Cresylecht violet, meldola blue and neutral violet penetrate easily, but did not give good differentiation on this material.

Experimental infections. Rats and mice, used as experimental hosts for *Schistosomatium douthitti*, were infected by placing them in a battery jar with a small amount of water containing cercariae obtained from either naturally or experimentally infected snails. Cercariae from several snails were used for infecting each animal in order that both males and females would be present. The water containing the cercariae was always heated to a temperature varying from 30° to 36° C. because the larvae are more active at these temperatures. The animal to be infected was allowed to stand in the water for a short period of time. The same method of infection was used on all other animals tried as experimental hosts with the exception of one cat. This cat from which several undeveloped worms were later recovered was infected by cercariae in its drinking water.

Snails which were to be infected with the miracidia of *S. douthitti* were placed singly in shell vials and to each vial was added one or more miracidia. These miracidia were obtained by collecting the

feces of infected mice and placing them in water* where the eggs hatched after a short time.

Life history.

Adult worms of this species live in the hepatic portal veins of mice, the females depositing their eggs in the small veins along the intestine. The eggs pass through the intestinal wall, during which time development takes place and reach the exterior in the feces of the host. If the feces are deposited in water, the eggs hatch in a short time and the miracidia swim actively about. If a suitable snail is present one or more miracidia may penetrate into this host. After penetration, a miracidium transforms into a mother sporocyst which in turn gives rise to daughter sporocysts. Daughter sporocysts give rise to cercariae which leave the snail and swim about in the water. If a mouse is present, the cercariae penetrate through the skin of this host and make their way along the blood stream to the hepatic portal veins where they reach maturity. This entire life history was completed experimentally in the laboratory, and its various aspects will be considered in detail under the following heads: Intermediate host, definitive host, adult male, adult female, egg, miracidium, mother sporocyst, daughter sporocyst, cercaria and longevity of adults.

Intermediate host.

Cort (1915) in his original description of *Cercaria douthitti* gave *Lymnaea reflexa* Say collected near Chicago, Illinois, as the intermediate host of this cercaria. During a survey of the fork-tailed cercariae in the Douglas Lake region of Michigan, Cort (1918) found *Cercaria douthitti* to be present also in *Lymnaea stagnalis appressa* (Say), *Lymnaea stagnalis perampla* Walker and *Physa ancillaria parkeri* (Cuvier). Miller (1926) likewise reported having found this cercaria in *Lymnaea stagnalis* var. *appressa* from the same region. In the vicinity of Ann Arbor, Michigan, where all of my own collections have been made, *C. douthitti* has been found in *Lymnaea stagnalis appressa* (Say), *Lymnaea palustris* Müller and *Physa gyrina elliptica* Lea. Thus six species of snails are known to serve as intermediate hosts for *Cercaria douthitti*. The striking lack of specificity of this larval trematode in the choice of an intermediate host was pointed out by Cort (1918).

Definitive host.

Adult worms, both males and females, were originally obtained from experimentally infected white rats and several subspecies of deer mice of the species *Peromyscus maniculatus* (Wagner) Bangs (1898).

In later experiments *Mus musculus* Linnaeus and *Microtus pennsylvanicus pennsylvanicus* (Ord) Rhoads (1895), served as definitive hosts.

During the summer of 1929 small mammals were trapped in the vicinity of Third Sister Lake, near Ann Arbor, with the hope of finding the natural host of *S. douthitti*. This area was selected because many snails collected from this particular locality were infected with *Cercaria douthitti*, the larval stage of this parasite. Thirty-six mammals were caught in the traps. These included one weasel, *Mustela novaborasensis novaborasensis* (Emmons) Miller (1912), thirteen masked shrews, *Sorex cinereus cinereus* (Kerr) Jackson (1925), eleven short-tailed shrews, *Blarina brevicauda talpoides* (Gapper) Bangs (1902), and ten meadow mice, *Microtus pennsylvanicus pennsylvanicus*. Of the latter species, two were found to be infected with mature *Schistosomatum douthitti*. One of the *Microtus* contained a pair of copulating worms in a mesenteric vein of the caecum and the other had three males and one female in a similar position.

It is to be regretted that during the several weeks of trapping not a single *Peromyscus* was caught, although specimens of this genus had been trapped from the same locality on previous occasions by other students before this study was begun. Thus, it could not be determined whether members of the genus *Peromyscus* are naturally infected with *S. douthitti*, however, if mice of this genus frequent the water's edge, it is very probable that they will be found infected with this parasite. Mammalogists are of the opinion that these mice generally avoid water.

Of the species of mice employed for the experiments, one serves as a final host apparently as well as another. The eggs which have been deposited in the mesenteric veins by the female worms break through the intestinal wall into the digestive tract and reach the exterior in the feces of the host, thus completing this phase in the life history of the parasite.

While rats serve as hosts in which this parasite can live and mature, they can not be considered as normal hosts, for the eggs of the worm fail to break through into the lumen of the intestine. For this reason, even though rats might receive a natural infestation the life cycle of the parasite could not be completed.

Two cats were tried as experimental hosts. In one of these, four male and five female worms were recovered from the portal system. One male worm which held two females in the gynecophoric canal was recovered from the liver of the cat, and three pairs of copulating worms were taken from the mesenteric veins along the duodenum.

The cat from which these worms were taken was killed forty-five days after the first attempt at infection and forty-one days after the last. The worms should have been mature, but instead all were small and immature. Apparently they had reached the maximum size which they could attain in this host. The reproductive organs in the males appeared mature, but there were no eggs in the uterus of the females. The very fact that this parasite could not mature in this animal is sufficient to rule out the cat as a normal host.

A young weasel, *Mustela novaborasensis novaborasensis*, two muskrats, *Ondatra zibethica zibethica* (Linnaeus) Miller (1912), two ducklings and two painted turtles, *Chrysemys belli marginata*, were tried as experimental hosts but were found upon subsequent examination to be entirely negative and thus can not be considered to serve as hosts for *Schistosomatium douthitti*.

Adult worms.

Worms *in copula* were taken from the portal veins of the host twenty-two days after infection at which time masses of eggs were found in the small veins on the intestine. These worms were mature although they might not have reached their maximum length. Adult worms were always recovered from the hepatic portal system, either in its branches from the viscera where the worms descend to deposit their eggs or in the intra-hepatic vessels. In experimentally infected rats the infection was often so great that all the worms present could not possibly be located in the visceral branches of the portal vein and in such instances the intra-hepatic branches were so packed with worms as almost to stop the flow of blood. There was always a great variation in the size of worms from different hosts of the same species. This variation is apparently caused by differences in the intensity of the infections. The worms are smaller in the heavy infections than in the light. Male and female worms taken from the extra-hepatic branches of the portal veins were usually paired, the female worm being held in the gynecophoric canal of the male. On a few occasions two females were found clasped by a single male. As Faust (1924) observed for *Schistosoma japonicum*, the anterior end of the male is usually directed against the blood current.

Adult male.

Size and form. Adult males (plate 1, fig. 1) vary greatly in size. Seventy worms taken from the portal veins of white rats measured 1.900-4.525 mm. in length (average 3.073 ± 0.048 mm.). Nine males

from two *Peromyscus maniculatus* measured 2.872–5.270 mm. in length and six males from two *Microtus pennsylvanicus* measured 4.050–6.339 mm. in length. Ten males from two *Mus musculus* measured 2.494–5.227 mm. in length. The preceding measurements were all made on preserved specimens which had been recovered from experimentally infected hosts. The single male worm taken from a naturally infected *Microtus* measured 6.336 mm. in length while the three worms recovered from a second naturally infected *Microtus* measured 3.088 mm., 4.568 mm. and 5.356 mm. respectively.

The body of the male worm is divided into two distinct parts, a forebody and a hindbody. The forebody in the seventy specimens taken from rats measured 0.799–1.738 mm. in length (average 1.310 mm.) and the hindbody measured 0.820–3.445 mm. in length (average 1.760 mm.) or a little less than three fifths of the entire body length. The mean width of the forebody immediately posterior to the ventral sucker was 0.237 mm., the mean width of the hindbody, 0.432 mm. The hindbody in living worms is folded to form a gynecophoric canal.

Suckers. An oral and a ventral sucker are present. The oral sucker is the smaller and has an average length of 0.109 mm. and an average width of 0.105 mm. The ventral sucker has an average diameter of 0.135 mm. It is stalked and can be extended and withdrawn, the cup-shaped part being able to assume many different forms.

Movement. Male worms exhibit a characteristic movement when placed in normal salt solution after removal from the blood vessels of the host. This movement is shown in plate 1, fig. 28, by a series of eight small sketches traced from consecutive pictures taken by a micro-cinema apparatus. The anterior end of the worm broadens out and is bent backward (A) while that part of the forebody posterior to the ventral sucker becomes narrowed. The anterior end then becomes gradually narrower and straightens out in a line with the rest of the body (B, C, D), while the posterior part of the forebody again becomes wider. As the anterior end again becomes wider and the oral sucker is bent ventrally until it touches the acetabulum, the posterior part of the forebody becomes gradually narrower (E, F, G, H). During these movements of the forebody, waves of contraction pass along the hindbody whose posterior end is often bent slightly backward.

Spination. Spines are distributed over the greater part of the surface of the body. Minute retrorse spines (plate 1, fig. 3, A) cover the lateral parts of the dorsal and ventral surfaces of the forebody

and extend mesad to the intestinal ceca, leaving the median part of each surface without spines. Small spines completely cover the oral sucker but are distributed on the ventral sucker as shown in plate 1, fig. 4. The ventral surface of the hindbody which forms the lining of the gynecophoric canal is densely covered with spines several times larger than those on the forebody and shaped as shown in plate 1, fig. 4, B. These spines are all directed mesad except those in a median position which are directed anteriorly and which undoubtedly aid in holding the female in position in the canal. Small spines like those on the forebody cover the edges of the dorsal surface of the hindbody, but large, blunt spines (plate 1, fig. 4, C) are scattered over the greater part of this surface. The spines on the forebody and those on the dorsal surface of the hindbody very likely assist the ventral sucker in maintaining the position of the worm in the vein against the blood current.

Digestive system. The digestive system consists of a mouth, an esophagus, two intestinal ceca and esophageal glands. The mouth is situated at the posterior end of the oral sucker and opens into a long esophagus whose mean length is 0.490 mm. This structure has thick muscular walls and becomes gradually wider toward its posterior end. Unicellular esophageal glands (plate 1, fig. 1, esg) of irregular and indistinct outline surround the esophagus. The glands surrounding the posterior half of the esophagus are many times larger than those around the anterior half. Immediately in front of the acetabulum, the esophagus bifurcates into two intestinal ceca which have many lateral diverticula. The ceca unite near the posterior end of the body into a single short gut. Anterior to this union there are always one or more transverse commissures (tc). The gut in living worms is always filled with partly digested blood which has a black appearance and makes the worm conspicuous while it is still in a vein. Various anomalies of the gut may be found. One male had a single intestinal cecum extending from the esophagus past the acetabulum and to the posterior end of the body, while in another the intestinal ceca had united a short distance posterior to the ventral sucker into a single gut which extended to the posterior end of the body. In one specimen, there was a transverse commissure between the intestinal ceca at the posterior end of the forebody.

Excretory system. The excretory system consists of two ducts, one situated lateral to each intestinal cecum. These ducts unite near the posterior end of the body into an extremely short, common duct which discharges exteriorly through a terminal excretory pore. In

living specimens one can observe cilia extending along the greater part of the length of the lateral ducts.

Reproductive system. The reproductive organs of the male (plate 2, fig. 6) consist of testes, vas deferens, cirrus, cirrus-pouch and seminal vesicle. The testes (t) are situated between the intestinal ceca at the anterior end of the hindbody and are composed of fifteen to thirty-six follicles, the exact number being difficult to determine. Each follicle opens through a short vas efferens into a single median vas deferens which extends anteriorly into the posterior part of the forebody, where it opens into a seminal vesicle (sv). This, together with a cirrus (c) is enclosed in a cirrus pouch (cp). The genital pore is situated ventrally at the anterior end of the left fold of the gynecophoric canal. When *in copula* the female worm is held in the gynecophoric canal with its dorsal surface against the ventral surface of the male and with only its anterior end including the ventral sucker protruding. In such an arrangement, the genital pore of the female which is immediately posterior to the ventral sucker is in a position exactly opposite the genital pore in the male.

Discussion. The adult male of this species is similar in many respects to the adult male of *Schistosomatum pathlopticum* Tanabe. Both have the body divided into a distinct anterior part occupying about two fifths of the entire length of the worm, and a hindbody which forms the gynecophoric canal and occupies about three fifths of the entire length. The digestive systems in the two species are essentially alike but in *Schistosomatum douthitti* there are always one or more transverse commissures anterior to the union of the intestinal ceca. The excretory systems are similar, and in both species the testes consist of more than fourteen follicles situated at the anterior end of the hindbody. The chief differences between the two species are in total length and character of the reproductive organs. Tanabe (1923) gave the length of male worms of *S. pathlopticum* as 5.6–11.8 mm. Males of *S. douthitti* measured from 1.900–6.339 mm. in length, the maximum length of the latter species exceeding the minimum length of the former by less than one millimeter. Tanabe (p. 192) stated that the number of testes in *S. pathlopticum* was "about fourteen to eighteen, usually sixteen in number" and that the posterior arm of the seminal vesicle which is semilunar in shape "is directed median and forward as the ductus ejaculatorius." Tanabe also stated (pp. 192–193) that, "The genital pore (is) situated at the midline or a little toward the left side of the beginning part of the gynecophoric canal." There are from fifteen to thirty-six testes in males of *S.*

douthitti although the number is usually difficult to determine and instead of a ductus ejaculatorius, a cirrus and cirrus pouch are present. The genital pore in the present species is always situated ventrally and on the left side at the anterior end of the gynecophoric canal.

Adult female.

Size and form. The female worm is filiform (plate 1, fig. 2) and when mature is usually found in the gynecophoric canal of the male. It is usually shorter than the male. Fifty females taken from white rats measured 1.641–3.553 mm. in length (average 2.48 ± 0.46 mm.). Eleven females from two *Peromyscus maniculatus* measured 2.538–4.320 mm. in length and eighteen females from two *Microtus pennsylvanicus* measured 1.315–4.784 mm. in length. Nine females from two *Mus musculus* measured 1.138–3.682 mm. in length. The preceding measurements were made on preserved specimens recovered from experimentally infected hosts. The single female taken with a single male from a naturally infected *Microtus* measured 4.816 mm. in length, and another female taken with three males from a naturally infected *Microtus* measured 5.356 mm. The mean width of the specimens taken from rats was 0.134 mm. just posterior to the ventral sucker and the mean width taken one third of the distance from the posterior end was 0.154 mm.

Suckers. Both oral and a ventral sucker are present. The oral sucker is the smaller and has an average length of 0.070 mm. and an average width of 0.065 mm. The ventral sucker is stalked and has an average diameter of 0.076 mm.

Movements. When free in normal salt solution the anterior end of the female including the acetabulum exhibits movements similar to those which the anterior end of the male exhibits under similar conditions.

Spination. The spines on female worms are limited in distribution. Small, posteriorly directed spines cover the lateral edges of the dorsal and ventral surfaces extending from the anterior end of the body posteriorly to the beginning of the ovary. The median parts of these surfaces are unspined. Spines are distributed over the whole surface of the oral sucker but on the ventral sucker their arrangement is like that on the acetabulum of the male (plate 1, fig. 4).

Digestive system. The digestive system resembles that of the male and has the same parts. The intestinal ceca are wider than in the male and since they hold more blood, the female is always more conspicuous in the veins than the male. The mouth opens into a long,

muscular esophagus which has a mean length of 0.166 mm. Esophageal glands resemble those in the male both as to size and distribution. The bifurcation of the esophagus occurs immediately in front of the acetabulum. The ceca are at first irregular, but posterior to the ovary many lateral diverticula are present. As in the male, the ceca unite near the posterior end of the body into a short single gut anterior to which are one or more transverse commissures.

Reproductive organs. The reproductive organs consist of ovary, oviduct, vitellaria, vitelline duct, seminal receptacle, oötype, Mehlis' gland and uterus. The ovary is spiral (plate 2, fig. 5, ov) and is situated on the right side in the anterior half of the body. At its posterior end the ovary is connected with the oviduct (ovd) which turns anteriorly, extending forward to the oötype (oo). A seminal receptacle (sr) is located near the origin of the oviduct. No Laurers' canal was observed. The vitellaria (v) lie between and lateral to the intestinal ceca packing the posterior three fifths of the body with the exception of the extreme posterior end. There are two vitelline collecting ducts (vtc), one ventral to each intestinal cecum, which unite at the anterior end of the vitellaria into a common vitelline duct (cvt). This duct in mature worms is often much distended with yolk cells. The common vitelline duct and the oviduct unite immediately before entering the oötype, the place of union being surrounded by the Mehlis' gland (mg). Anterior to the ovary is the oötype, oval in shape and lined with relatively large cells, each containing a conspicuous nucleus. The oötype opens through a short uterine duct into a long, muscular uterus (ut) which discharges through a genital pore (plate 1, fig. 2, gp) situated just posterior to the acetabulum. The uterus in mature worms is packed with numerous eggs.

Discussion. The female of *S. douthitti* differs from the female of *S. pathlocopticum* chiefly in length and in details of the reproductive apparatus. Tanabe (1923) gave the length of females of the latter species as 4.5–10.2 mm. Females of the present species measure 1.138–5.356 mm. They also always have one or more transverse commissures anterior to the union of the intestinal ceca, and an oötype and a seminal receptacle. Tanabe did not mention observing these structures in the female of his species.

Egg.

Undeveloped egg. The eggs of *Schistosomatium douthitti* are entirely undeveloped when deposited and are much smaller than those that have passed through the intestinal wall of the host and contain

mature embryos. Fifty eggs which had been extruded from the uterus of female worms after the latter had been removed from the mesenteric veins and placed in normal salt solution measured 0.042–0.080 mm. in length (average 0.056 mm.) by 0.030–0.058 mm. in diameter (average 0.039 mm.). All measurements were made on eggs which had been in saline solution from thirty minutes to one hour.

The eggs are oval in shape (plate 2, fig. 10) and have a thin, transparent and elastic shell. There are no markings of any kind on the shell, and no spine is present as there is on the eggs of nine of the twelve previously described species of schistosomes parasitic in mammals. For one species the eggs have not been described. The eggs of two species, *Schistosoma faradjei* Walkiers (1928) and *Schistosomatium pathlocopicum* Tanabe (1923), are spineless. To this group must now be added *Schistosomatium douthitti*, making a total of three which have spineless eggs.

There is a slight indentation at the smaller end of eggs of *S. douthitti* which have just passed from the uterus. This is not visible in eggs containing fully developed miracidia. Undeveloped eggs contain an ovum (o) and usually from eight to eleven yolk cells. The yolk cells are large and somewhat flattened, and contain a conspicuous nucleus. Each cell is filled with yolk material. The ovum has no particular location within the eggshell and may be found in the midst of the yolk cells or in a more peripheral position.

Developed egg. A number of days necessarily elapse from the time of deposition of eggs in the blood vessels and their appearance in the feces of the host. Masses of eggs are present in the mesenteric veins of the host twenty-two days after infection and a few immature eggs may usually be recovered from the feces twenty-eight to thirty days after infection. These facts indicate that a minimum of six to eight days is necessary for the accumulation of eggs and their passage through the intestinal wall. Eggs containing mature miracidia ordinarily are not found in appreciable numbers until thirty days after infection.

When placed in water, eggs containing mature embryos (plate 2, fig. 11) swell immediately. Fifty eggs after being one to two hours in water measured from 0.094–0.122 mm. in length (average 0.108 mm.) by 0.074–0.098 mm. in diameter (average 0.082 mm.).

The mature miracidium is readily visible inside the transparent shell and is surrounded by a transparent liquid. On one side of the miracidium there are two round or oval globules. Surrounding these and the miracidium is a thin covering, the vitelline membrane (vm).

Between this membrane and the egg shell is a much denser liquid filled with small granules.

Hatching. The hatching of the egg has been described by several investigators. Most of the observations were made on the eggs of *Schistosoma haematobium*. My findings on the eggs of *S. douthitti* agree essentially with those made on other species by previous workers who observed that the eggs swell immediately after coming in contact with water, the hatching being caused either by the absorption of water or by the activity of the miracidium or by both. There is no unanimity of opinion as to which of these factors is of the greatest significance in the actual freeing of the miracidium from the shell. Some observers think that both factors are important while others consider the one or the other of more significance. I believe that both factors play a part in the hatching process. The swelling of the egg gives a larger space for the activity of the miracidium which perhaps is stimulated by the increase of pressure within the egg shell and perhaps by change of temperature. Since undeveloped eggs do not burst open, it seems probable that the movements of the mature embryo and possibly secretions emitted by the embryo may aid in the splitting of the shell. Cobbold (1872:91), Brock (1893:624), Seligmann (1897:388) and Conor (1910:532) have all stated that in the eggs of *Schistosoma haematobium* the break in the shell appears along the longitudinal axis. Railliet (1892:163) working on the same species stated that the break occurs usually "dans le voisinage de la région céphalique." Cort (1919) presented a photomicrograph showing the miracidium of *Schistosoma japonicum* which has just escaped from the shell through a slit across the end. During the present study all the eggs observed in a depression slide under a cover glass had split across the end, yet every egg which had hatched in a watch crystal of water and consequently without outside pressure had a longitudinal slit. Apparently the pressure of the cover glass has something to do with the position of the break in the shell. When the slit appears along the side of the egg, the parted edges of the elastic shell roll back. The ciliated larva, now liberated from the shell, extends and contracts its body until free from the granules which surround it and then swims away through the water.

Miracidium.

Form and measurements. A free swimming miracidium of this species is somewhat pyriform in shape (plate 2, fig. 13) although it possesses the ability to modify its form greatly by contraction and

extension of its body. In the center of the anterior end there is a rounded projection, the apical or anterior papilla (plate 2, fig. 12, ap). Ten miracidia which were placed individually in drops of water on a slide and killed with heat had an average length of 0.131 mm. and an average width at the greatest diameter of 0.060 mm.

Complexity of organization. Judging from the published descriptions and figures one might consider the organization of a miracidium to be relatively simple, but the number of organs and systems of organs or their primordia present in the miracidium of this species is evidence of a complex organization. The presence of an epidermal covering of cilia for locomotion, a primitive gut, well developed glandular apparatus, an excretory system, many reproductive cells and a complex nervous system, together with other structures whose functions are unknown, indicate complexity, not simplicity of organization. Comparatively little detailed descriptive work has been done on the miracidium stage of trematodes up to the present time, but so far as possible structures of various species are here compared with those of the miracidium of the present species.

Epithelium. Almost the entire outer surface of the body of the miracidium is covered with cilia which arise from twenty-one flattened epidermal cells. These cells, referred to by Ortmann (1908 : 268) as "Plattchen," are arranged in four transverse rows (plate 2, fig. 12). The spaces between these cells, as well as the anterior papilla, are not ciliated. In early stages of development the cells are rounded and appear as Thomas (1883: plate 2, fig. 7, Z) has figured them for miracidia after penetration into the snail host. The first row contains six cells (fig. 12, ep), the second eight (ep₂), the third four (ep₃) and the fourth three (ep₄). The cells of the first row are somewhat triangular in shape, their apices being situated at the base of the apical papilla (ap) and their bases at the level of the lateral processes (lp). The cells in the second row (ep₂) are much longer than any of the other epidermal cells and are rectangular in shape with rounded corners. They extend posteriorly a little beyond the center of the body. The cells of the third row (ep₃) are almost as wide as long and have strongly rounded corners. The cells of the posterior row (ep₄) are cuneiform, their bluntly pointed ends directed posteriorly. The epidermal cells of the first two rows are situated close together, being separated by narrow nonciliated areas, while the cells of the last two rows are far apart and are separated by wide nonciliated areas. These nonciliated areas separating the ciliated epidermal cells are the exposed parts of a subepithelial layer upon which the epidermal cells

rest. Sewell (1922: 286) erroneously interpreted these areas as "the outlines of a system of minute canals running between the epithelial cells." The character of this layer will be taken up later.

The cilia covering the surfaces of the posterior three rows of cells are approximately 0.018 mm. in length while those on the cells of the first row vary gradually from 0.018 mm. at the posterior ends of the cells to not more than one fourth this length at the anterior ends of the cells (plate 2, fig. 13). A definite arrangement of cilia as Ortmann (1908: 270, Taf. 14, fig. 34a) described and figured them in the miracidium of *Fasciola hepatica* was not observed.

In early developmental stages, before the ciliated epidermal cells have become flattened, the nucleus in each cell may be observed as a more or less rounded structure, but these could not be observed in mature miracidia even with the aid of *intra vitam* stains. Permanent mounts were not made, so it could not be determined whether the nucleus of each ciliated ectodermal cell of the miracidium of *S. douthitti* is spherical as figured by Leuckart (1894, figs. 37, 44), Thomas (1883, plate 2, fig. 5) and Ortmann (1908, Taf. 14, figs. 32, 33, 38) for the miracidium of *Fasciola hepatica* or narrow and elongated with irregular outline as figured by Coe (1896, fig. 1) for the same species.

The number and arrangement of the ciliated epidermal cells have never been described for the miracidium of any other schistosome, including the well known human forms. However, statements in the literature and a comparison of the figures of other schistosome miracidia with the appearance of the miracidium of *S. douthitti* under various conditions afford indirect evidence that epidermal cells are present in other species of schistosomes and that they are probably arranged in the same number of rows as described for the miracidium of the present species. When numbers of miracidia of *S. douthitti* are studied under various states of contraction, it is noted that constrictions occur in definite places agreeing with the intercellular spaces between the transverse rows of epidermal cells. The position of these constrictions is determined by the fact that the epidermal cells are somewhat rigid while the intercellular areas are much less rigid. There are then three definite places for transverse constrictions and a depression at the end of the body where the ends of the cells in the last row are separated from each other. With these facts in mind the observations of other workers may be interpreted.

Harley (1871, plate 1, fig. 8) observed three constrictions on the miracidium of *Schistosoma haematobium* concerning which (p. 56) he remarked: "There is a distinct segmentation of the body, a character

which is foreshadowed in the constrictions which affect the living embryos, and which no doubt determines the regularity of these." Railliet (1892: 162) made the following statement concerning the miracidium of the same species: "Le corps offre trois étranglements: deux au niveau des ceintures signalées plus haut, et une troisième plus en arrière, vers le sixième postérieur du corps." Brock (1893: 623) working on the same form stated that the regularity of the cilia "is interrupted at two situations, where certain lateral apertures are placed around the body, thus dividing the surface into three zones—cephalic, caudal and intermediate. . . . At the extremity of the caudal end, . . . a slight depression generally exists." Sewell (1922: 288) working on the miracidium of *S. haematobium* stated: "At the extreme anterior end is an apical papilla, which is devoid of cilia; all the rest of the surface of the body is covered with long cilia, except along certain lines which appear to correspond with the lines of junction of the epithelial cells." His figure (plate 32, fig. 3) shows clearly the lines of junction between the second and third, and the third and fourth rows of epidermal cells. In the miracidium of *S. douthitti* the first and second rows of cells are separated at the level of the lateral processes (plate 2, fig. 12, lp). If this is true for the miracidium of *Schistosoma haematobium*, then four rows of epidermal cells must also be present in that species. Reisinger (1923: 12) actually observed epidermal plates on the miracidium of *S. haematobium*, although he was not able to determine their number and arrangement.

Cort (1919) mentioned nothing of ciliated epidermal cells on the miracidium of *Schistosoma japonicum*. Faust (1924) in a monograph on the same species figured certain structures (plate 2, fig. 11, nt) which he interpreted (p. 28) to be nerve trunks, but expressed some doubt about this interpretation by adding: "These may be the cords which Sewell (l. c.) has regarded as epithelial excretory tubules, since the number and distribution correspond almost part for part." These "cords" both in position and arrangement appear much like the spaces between the epidermal cells in the second row and the areas between these "cords" have a shape very similar to the epidermal cells in the same row. It is my interpretation that the cords are in fact the spaces between ciliated epidermal cells. Tanabe (1923, plate 15, fig. 7) figured a miracidium of *Schistosomatium pathlocopicum* in which there are three constrictions and a terminal depression corresponding in position to the constrictions and the depression which may be seen in eggs of *S. douthitti*. In my opinion these modifications of the normal form are undoubtedly produced in the manner explained

by me for *S. douthitti*. From these observations one may assume with some degree of safety that further investigation on the miracidia of the various above mentioned schistosomes, and perhaps of all schistosomes, is likely to reveal the presence of ciliated epithelial cells similar to those described for the present miracidium.

Coe (1896) described the miracidium of *Distomum hepaticum* (*Fasciola hepatica*) as having definitely twenty-one ciliated epidermal cells arranged in five transverse rows. Leuckart (1882) and Thomas (1883) had previously given incomplete descriptions of these cells in the same species. Coe mentioned nothing of occasionally seeing six rows of cells as did Thomas. Ortmann (1908) confirmed Coe's work in respect to the number and arrangement of the epidermal cells in this species. Looss (1892, plate 19, fig. 17) figured ciliated epidermal plates on the miracidium of *Amphistomum subclavatum*, but he did not give their number and arrangement. Sewell (1922) observed the presence of ectodermal cells in the miracidium of *Cercaria Indicae* XV, but he did not determine their number. Barlow (1925: 20) found the epidermal pattern of *Fasciolopsis buski* to be "made up of five tiers of six hexagonal plates each." Mathias (1925) observed twenty-one ciliated ectodermal cells in the miracidium of *Strigea tarda*, and Van Haitsma (1931) observed the same number for the miracidium of *Diplostomum flexicaudum*. The arrangement of these cells in the two latter species corresponds exactly with that found in *Schistosomatium douthitti*. The similarity in both the number and arrangement of the ciliated epidermal cells in the miracidia of these three trematodes appears to be another fact in support of the claim for relationship between the two families, the *Strigeidae* and the *Schistosomatidae*, of which the three forms are representatives. La Rue (1926) first pointed out the other facts in support of such a relationship.

The value of the number and arrangement of ciliated epidermal cells as criteria in fixing relationships between families or larger groups can be determined only by more extensive investigations. Thus, while it is interesting to note that the miracidia of several different species of digenetic trematodes possess the same number of such cells although not the same arrangement, there are such significant differences in the cercarial stages and elsewhere that the coincidence of finding the same number of epidermal plates in the miracidia cannot be held to be of much significance.

Subepithelium. Beneath the ciliated epidermal plates is a subepithelial layer (fig. 13, se) which Leuckart (1882: 92) designated as the body wall in the miracidium of *Fasciola hepatica*. The subepi-

thelium is composed of a single layer of clear cells and only occasionally can a nucleus be seen. This layer is continuous over the entire body and it extends slightly outward filling the intercellular spaces of the epidermal layer. None of the exposed part of the subepithelial layer is ciliated. Leuckart (1882), Thomas (1883), Coe (1896) and Ortmann (1908) mentioned the presence of this layer in the miracidium of *Fasciola hepatica*. Leuckart (1882:91) and Van Haitsma (1931) noticed that the ciliated ectodermal cells are easily detached from the subepithelium and Barlow (1925) observed that the ciliated epidermal cells on the miracidium of *Fasciolopsis buski* were cast off during penetration of the larva into the snail host. If this is true then the subepithelial layer becomes the body wall of the mother sporocyst.

Muscles. The presence of circular and longitudinal muscle fibers as described by Leuckart (1882: 92), Thomas (1883: 111), Looss (1894: 524), Ortmann (1908: 270) and Faust (1924: 29) for other species of miracidia were not observed in the miracidium of *S. douthitti* with the methods of study employed.

Rows of cells. Two longitudinal rows of relatively large cells, one dorsal and one ventral in position (plate 2, fig. 14), are situated just below the subepithelium. These rows of cells extend from the base of the anterior papilla to near the posterior end of the body, the cells anterior to the brain (br) being spherical and arranged in a double row while the remainder are rectangular and arranged always in a single row. There are usually twelve each of round and rectangular cells although the number of each is somewhat variable. The function of these cells is at present wholly problematical and perhaps can be determined by studying their development in the embryo or by studying preparations of miracidia after their penetration into the snail host.

Gut. A sac-like structure, the so-called primitive gut (fig. 13, gs), which is filled with coarse granules, extends posteriorly from the apical papilla, slightly beyond and ventral to the anterior part of the brain. The anterior end of the gut is situated in the center of the apical papilla, but there is no true oral opening and the contents of the gut apparently have no special function during the free swimming life of the miracidium. It is possible that Reisinger (1923: 15) may have been correct in attributing to the contents of this structure an important function in the penetration of the miracidium into the snail host.

Glands. A large unicellular gland is situated on each side of the gut (fig. 13, pg) and opens through a wide duct at the base of the

apical papilla. Looss (1894: 524) quoted Brock as being the first to point out these glands as structures entirely independent of the gut-sac. As a matter of fact, Harley (1871) had recognized them as independent structures before Brock. These glands have been given various names, among which probably the most common is penetration gland. In the center of each is a conspicuous nucleus. Each gland and its duct is filled with coarse granules like those in the most anterior pair of penetration glands of *Cercaria douthitti* before its emergence from the snail host. In fact in structure and appearance they somewhat resemble the penetration glands of forked-tailed cercariae.

Lateral processes. A pair of lateral processes (fig. 13, lp), projecting knob-like structures which have been previously described for the miracidia of several schistosomes and for the miracidium of *Diplostomum flexicauda* by Van Haitsma (1931), is situated, one on either side of the miracidium between the first and second rows of ectodermal cells. It was difficult to make out any internal structures connected with these processes but sometimes there appeared to be a duct extending inwardly and posteriorly from each process. These ducts seemed to terminate in a slightly enlarged vesicle attached to the brain. Cort (1919) and Faust (1924) termed these processes anterior or lateral ducts in the miracidium of *Schistosoma japonicum* and both stated that the extrusion of substances from these structures was observed. The present observations agree with those of Sewell (1922: 287) who "could detect no trace of any orifice opening on the surface," and hence found no justification for the terms anterior or lateral ducts. No substances were ever seen extruded from these structures in the miracidium of *Schistosomatium douthitti*. Since, as previously stated, Sewell's idea concerning the presence of "minute canals running between the epithelial cells" is considered erroneous, no confirmation was obtained for his impression (1922: 287) "that the so-called anterior ducts are vesicular swellings on the course of the anterior circular ectodermal canal. . . ." Reisinger (1923) described the lateral processes as sensory papilla.

Lateral papillae. Two small lateral papillae, which sometimes appear as a single structure, are situated midway along the posterior border of each ciliated epidermal cell in the first row. These structures are visible only when in a lateral position (fig. 13, lpa) and the arrangement is such that a group of two papillae is always visible anterior to each lateral process. Coe (1896) observed similar papillae, except that they were single instead of two, in the miracidium of

Fasciola hepatica. Van Haitsma (1931) observed a single papilla (small lateral process) anterior to each large lateral process in the miracidium of *Diplostomum flexicaudum*. No openings from these papillae could be seen. Looss (1894: 523, 524) and Reisinger (1923: 17-19) claimed to have found not only an anterior row of papillae but also a posterior row in the miracidium of *S. haematobium*. Reisinger suggested that these small papillae as well as the large lateral processes may be sensory in function. His interpretations will be discussed later.

Nervous system. The nervous system of *S. douthitti* consists of a central nerve mass or brain (fig. 12, br), two lateral nerves (fig. 13, ln) and two groups of bipolar sensory cells, both situated anterior to the brain (fig. 12, asc, psc). The interpretation that these cells are sensory in function is based upon the fact that each cell has one termination on the surface of the body and another in the brain. Thus not only in appearance but in their arrangement they fulfil the essential requirement of sensory cells. Neither eyespots, pigmented or unpigmented, nor lenses are present.

The brain (fig. 13) is located near the center of the miracidium and may appear bilobed. Over its surface are numerous cells whose nuclei are easily stained with brilliant cresyl blue or neutral red. The center of the brain is fibrous (fn). Some of these fibers extend outwardly on each side as a lateral nerve (ln) which forks before reaching the body wall. These nerves are similar to those described by Ortman (1908) for the miracidium of *Fasciola hepatica*. They have not, however, been subjected to any special neurological technique. At the anterior end of the miracidium are three pairs of bipolar sensory cells (fig. 12, asc), two pairs situated lateral to the duct of each penetration gland and one pair usually between the two ducts. In well stained specimens, the cells on each side may occasionally be seen to be connected with each other by a network of fine fibers. One process from each cell extends posteriorly and enters the brain; the other extends anteriorly and terminates on the surface at the base of the head papilla. The anterior termination of each fiber is slightly enlarged. Coe (1896: 567) observed six to eight small circles lateral to the mouth opening in the miracidium of *Fasciola hepatica*. Since these structures have so much resemblance to the surface terminations of the fibers from the first tier of sensory cells in the miracidium of *S. douthitti*, it seems probable that they may be identical.

The posterior tier of sensory cells (fig. 12, psc) is situated between the brain and the level of the lateral processes. These cells are similar in appearance to the anterior sensory cells and each sends a long

fiber posteriorly which branches before entering the brain. The anterior fiber from each cell is coarser than the posterior. It terminates on the surface of the miracidium between the first and second rows of ciliated epidermal cells in an enlargement from which six or more stiff bristles project. The number of posterior sensory cells varies considerably. In twenty-five miracidia the number ranged from fourteen to twenty. Even in miracidia which have the same number of posterior sensory cells, the number present on the dorsal and ventral sides may vary. In a single miracidium the bristle patches or surface terminations of these cells may stand alone or may be arranged in groups of either two, three or four, or in combinations of such groups. There is always a bristle patch near each lateral process. The most definite arrangement of sensory cell terminations ever observed is shown in fig. 12. On both the dorsal and the ventral side were two groups of four bristle patches, between which was a single bristle patch. There was also a bristle patch on the ventral side near each lateral process. Other arrangements of bristle patches are shown in plate 2, fig. 9, A, B, C, D, E.

Looss (1894: 525) thought that on many occasions he had observed nerve fibers extending posteriorly from the brain in the miracidium of *Schistosoma haematobium*, but at other times such structures were not visible. Reisinger (1923), working on the same species, observed a large pair of nerves extending from the brain forward to the lateral processes (large sensory papillae) and a smaller, posterior pair of nerves which he was not able to follow to their terminations. He made the following statement (1923: 19) concerning the anterior pair of nerves and their relation to the lateral processes and papillae: "Allerdings erhielt ich bisweilen den Eindruck, als ob knapp unter jeder Papille einige feine Fibrillen vorbeizögen, die mit den Papillen verbunden seien und in ihrer Gesamtheit einen Nervenring darstellen, der im Bereich der grossen Sinnespapillen mit den Papillarnerven zusammenhinge. Sollte es sich, . . . einmal erweisen, dass eine solche Ringkommissur tatsächlich vorhanden ist, dann wird man auch die kleinen Papillen als Sensillen deuten können." Concerning the posterior pair of nerves he remarked (p. 19): "Es ist vielleicht nicht unmöglich, dass dieselben im wesentlichen dem hinteren Papillenkranze zustreben." Reisinger likewise observed extending anteriorly from the brain numerous fine fibers which he suggested might innervate the area surrounding the head papilla. I did not observe in the present species any nerves comparable to the two pairs described by Reisinger. Barlow (1925) claimed to have observed nerve filaments

in the miracidium of *Fasciolopsis buski* but gave no details concerning them. The structures which Faust (1924: 28, 29) described as possible nerve trunks have already been discussed.

Excretory system. The excretory system of the present miracidium is similar to those described for the miracidia of other schistosomes and strigeids. There are two pairs of flame cells, one located lateral to the penetration glands or central nerve mass and the other at the level of the posterior half of the third row of ectodermal cells (fig. 14, fc). An anterior and a posterior collecting tubule from the respective flame cells on each side of the body unite into a more or less convoluted collecting duct (cd). Each collecting duct, after making a loop to the posterior end of the body, opens into a small bladder (eb) which discharges through an excretory pore situated laterally in the area between the ciliated ectodermal cells comprising the third row of ectodermal plates.

Germ cells. Germ cells fill the greater part of the miracidium posterior to the brain (fig. 13, gc). These cells are relatively large and contain a nucleus with a conspicuous nucleolus. The very small germ cell nucleus figured by Cort (1919) and Faust (1924) in the miracidium of *Schistosoma japonicum* appears really to have been the nucleolus of these cells. The germ cells do not lie free in the body cavity of the miracidium as is generally supposed; but are attached to the body wall by fiber-like extensions of the cell body. In this way the germ cells maintain a constant position. Looss (1892) observed that the germ balls in the miracidium of *Amphistomum subclavatum* were likewise held in position by fiber-like attachments to the body wall.

Mother sporocyst.

Location. Mother sporocysts in various stages of development were obtained from experimentally infected snails of the species *Lymnaea stagnalis* and *Lymnaea palustris*, that had been anesthetized with chloretone. The worms were dissected out with fine needles. Mother sporocysts were always found in the head and neck regions of the snails, immediately dorsal to the esophagus and cerebral ganglia. Preserved specimens were mounted *in toto* and form the basis of observations on detailed structure.

Form and structure. The mother sporocyst is long and sac-like (plate 2, fig. 8). Individuals of the same age vary greatly in development, growth apparently being related to temperature conditions. The sporocyst is relatively simple in structure and consists of a thin body wall surrounding a cavity in which the germ balls develop.

The body wall has a different appearance in young and old sporocysts. In specimens seventeen days old it consists of a thin, outer cuticle (plate 3, fig. 18, cu) inside of which is a single layer of cells with distinct cell outlines. This layer is usually more than one cell in thickness at the ends of the sporocyst. Two principal kinds of cells are present, relatively large cells with a great amount of cytoplasm and small, darkly staining cells whose cytoplasm is drawn out into long processes (plate 3, fig. 24). A distinct nucleolus is present in the nucleus of some of the large cells. Those cells which contain this structure are identified as germ cells (gc), although the cells lacking it may also be potential germ cells. The small cells which likewise have a distinct nucleolus are scattered among the larger cells, and while they may be seen in an optical view (plate 3, fig. 18), their shape and position are best determined in surface views (plate 3, fig. 24).

Germ balls. The germ cells give rise to germ balls (plate 3, fig. 18, sgb) which, as growth proceeds, push out into the cavity of the mother sporocyst where they develop into daughter sporocysts. These germ balls are usually observed to be attached to the wall of the mother sporocyst by fibrous strands of tissue (plate 3, figs. 18 and 23, gba) until late stages in their development. Looss (1892) observed that the germ balls formed in the miracidium of *Amphistomum subclavatum* also remained attached to the body wall for some time. Mother sporocysts removed from snails seventeen days after infection were packed closely with germ balls, none of which were further developed than those shown in figure 18. The older germ balls are surrounded by a single layer of flat cells which Dubois (1928) referred to as the primitive epithelium.

Body wall. The body wall of sporocysts thirty-nine days old (plate 3, fig. 23) has a cuticle (cu) several times thicker than that of younger sporocysts and fine transverse lines can usually be observed in it. Cell outlines are difficult to distinguish in these older specimens and although germ balls in various stages of development are present (sgb), there are relatively few germ cells. Many daughter sporocysts have already matured and escaped from the parent worm into the lymph spaces in the liver of the snail. Longitudinal muscle fibers (lf) were observed, but the presence of transverse fibers could not be determined. Ssnitzin (1909) also found the muscle layers difficult to differentiate in the sporocysts of *Bucephalus polymorphus* and several related forms. No birth pore was observed.

Movement. When removed from the snail host and placed in normal salt solution, the mother sporocyst is capable of slight move-

ments that are visible under the microscope. Inability to exhibit more distinct movements is correlated with the poor development of muscle fibers.

Age. No mother sporocysts nor young daughter sporocysts were found in snails killed and dissected 134 days after infection, although all stages of developing cercariae were present. After the daughter sporocysts have emerged, the mother sporocyst disintegrates. The length of life of the mother sporocyst was not determined.

Daughter sporocysts.

Young daughter sporocysts were removed from the livers of snails thirty-six days after infection. At this time they were not more than one third of their adult length. They were elongated in shape (plate 3, fig. 22). The anterior end was covered with relatively large spines and the rest of the body, as observed under dark field illumination, was covered with short cilia. Miyairi and Suzuki (1914) working on the life history of *Schistosoma japonicum* were the first to observe spines on the anterior end of daughter sporocysts. When free in normal salt solution the sporocysts move slowly. The spinous anterior end is continually extending and contracting, and there is a slight progression forward accompanied by some turning on the longitudinal axis.

Structure. At this stage of development there is no visible cavity in the daughter sporocyst, and no great differentiation of cells has occurred. An outside cuticle was not observed. In older sporocysts (plate 2, fig. 7) a cavity has appeared but it is conspicuous only in the regions where germ balls (cgb) of cercariae are developing. The body wall in these regions has lost its cilia and now consists of a thin outer cuticle (plate 3, fig. 17, cu) and a single layer of cells which have a close resemblance to those found in the young mother sporocysts. These cells are best seen in a superficial view of daughter sporocysts which have been slightly expanded by the absorption of water (plate 3, fig. 16). Large germ cells (gc) and smaller, darkly staining cells with long fiber-like processes are present. Small round cells with little cytoplasm can also be observed. The cercaria germ balls are similar in all visible respects to the germ balls which give rise to daughter sporocysts. Daughter sporocysts containing many germ balls have no visible movements.

Cercaria.

This cercaria has been described by Cort (1915, 1917) and Miller (1924) as *Cercaria douthitti*. During the present study a few addi-

tional morphological details were observed and are here added to the facts presented in previous descriptions.

The cercaria is an apharyngeal, distome cercaria of the furcocercous, brevifurcate type with pigmented eyespots. Specimens were obtained from both naturally and experimentally infected snails, cercariae first emerging from the latter forty-four to fifty-four days after infection. The measurements of *C. douthitti* made by Cort (1915) and those made during the present study are included in the tables below. Measurements of similar parts are included in the first table while some additional measurements of my own are placed in a supplementary table. Cort gave only average measurements and stated (p. 10) that, "In fixing freed cercariae for toto mounts the best results were obtained by the use of hot solutions of Bouin's picro-aceto-formal or corrosive-acetic." The number of cercariae measured by him was not given. My own measurements were made on twenty-five cercariae which had been killed in a 10 per cent solution of hot formalin.

The width of the tail stem was taken at two places, shortly posterior to the attachment of the tail to the body and immediately anterior to the bifurcation of the tail, the positions of greatest and least width respectively. Width of the body was measured across the center of the ventral sucker. The entire length of a cercaria was obtained by adding the lengths of the body, the tail stem and the tail furcae and then subtracting the length by which the tail stem and body overlap, an amount which is of only slight significance, if any, when the varying conditions of contraction and extension are considered. These measurements show that the average length of the body and that of the tail stem is practically the same, and that the length of the tail furcae is a little more than one third of the total length of the tail. A comparison of the average figures in table 1 shows that the measurements made by Cort and the writer are with few exceptions in good agreement.

Movement. *Cercaria douthitti* remains more or less quiescent for some time after emerging from the snail host, with its body somewhat contracted and parallel with the surface of the water and its tail hanging downward at an angle which may vary from a few to more than ninety degrees. When actively swimming through the water, the cercaria turns on the longitudinal axis, often describing a circular movement with the whole body and progressing with a rapid vibration of the tail stem as described by Cort (1915). Progression is usually tail first, although occasionally the body may go forward. During intervals of inactivity following periods of active movement a cercaria may hang suspended in the water with the body downward and the

Comparative measurements in millimeters of Cercaria douthitti.

Measurements by		Length of body	Width of body	Length of tail stem	Width of tail stem	Length of tail furcae	Length of head organ	Width of head organ	Diameter of ventral sucker	Width of eyespot
Cort.	Average	0.190 mm.	0.067	0.220	0.025	0.089	0.057	0.045	0.025	0.007
Price	Average	0.204	0.068	0.210		0.096	0.076	0.048	0.025	0.007
	Minimum	0.186	0.057	0.186		0.080	0.067	0.038	0.019	0.006
	Maximum	0.240	0.081	0.234		0.110	0.082	0.062	0.028	0.009

Supplementary table of measurements in millimeters of C. douthitti.

Measurements by		Length of esophagus	Distance from mouth to anterior end	Distance from ventral sucker to anterior end	Width of tail stem just below attach- ment to body	Width of tail stem at forking	Length of entire body
Price	Average	0.071 mm.	0.028	0.131	0.031	0.020	0.504
	Minimum	0.057	0.024	0.111	0.025	0.014	0.460
	Maximum	0.086	0.033	0.148	0.038	0.030	0.544

furcae spread. When moving along the bottom it goes forward in measuring-worm fashion by means of oral sucker and acetabulum. This is in contrast to Cort's statement (1915: 50) that *C. douthitti* "was not able to take hold with the oral sucker," but agrees with his later observations (1919) on the cercaria of *Schistosoma japonicum*. This looping movement has been described by several investigators for various species of schistosomes.

Spines. Small retrorse spines cover practically the whole outer surface of the body, tail stem and tail furcae (plate 3, fig. 20). The spines on the body have a quincuncial arrangement and are more numerous on the head organ anterior to the attachment of the latter with the body wall than on the rest of the body (plate 3, fig. 15). The spines on the tail and tail furcae have no definite arrangement. A small area immediately surrounding the mouth (plate 3, fig. 25) and a narrow area forming a circle around the ventral sucker (plate 3, fig. 15, ws) are spineless. Penetration spines are discussed in connection with penetration glands.

Body wall. A tough cuticula from which the above mentioned spines project covers the whole surface of the body and tail. Under the cuticula of the body are layers of circular and longitudinal muscles which may be clearly seen in mounts of living cercariae. Filling in the spaces between all the organs of the body is a parenchymatous tissue. Six or more rows of large cells which have the form of muscle cells lie beneath the cuticula of the tail stem (plate 3, fig. 21). The body of each cell is drawn out anteriorly and posteriorly into a long fiber which is attached to the inner surface of the cuticula. These cells are situated obliquely to the longitudinal axis and each has a conspicuous nucleus. These cells are similar to the myoblast cells described by Bettendorf (1897) for several species of trematodes. Fiber-like extensions were not observed on the cells in the tail furcae.

Head organ. The head organ (plate 3, fig. 20, ho) occupies almost the anterior third of the body and as in other schistosome cercariae bears little resemblance to the adult structure into which it develops. At the anterior end of the head organ is a concavity, the so-called oral sucker (fig. 19, os) which, in living cercariae, is being constantly pushed out and withdrawn. The head organ develops into the muscular oral sucker of the adult worm. The posterior part of the head organ is strongly muscular (fig. 19, mw) and consists of a thick outer layer of circular fibers and a narrow inner layer of longitudinal fibers. The point of attachment of the posterior part of the head organ to the body wall is visible as a distinct line (fig. 19, j). A large head

gland or "oral" gland as Khalil (1922:30) has termed it, which is filled with coarsely granular material, occupies the center of the head organ (fig. 19, hg). This gland extends anteriorly to the center of the concavity of the head organ where Cort (1919:498) stated that it "opens almost exactly in the middle of the anterior tip." No opening or extrusions from this structure were ever observed by me. I am inclined to agree with the interpretation of Miyagawa (1916) whose paper is discussed by Cort (1919:498) that this is "an adaptive larval structure which has some function connected with penetration." The ducts which pass through the head organ lateral to the head gland will be discussed in connection with the penetration glands.

Ventral sucker. The ventral sucker is situated a short distance posterior to the middle of the body and is not stalked as it is in the mature worm (fig. 19, vs). It has only a slight ventral depression and within there are powerful muscle fibers.

Penetration glands. Five pairs of penetration glands are present in cercariae which have actively emerged from the snail host (fig. 19, pg₂, 3, 4, 5, 6), although six pairs are present in cercariae which have been dissected from the livers of snails (fig. 20, pg₁, 2, 3, 4, 5, 6). Cort (1915, 1917) and Miller (1924) observed only five pairs of glands. The six pairs of glands may be divided into three groups, the most anterior pair (pg₁) in the first group, the second and third pairs (pg₂ and pg₃) in the second group and the fourth, fifth and sixth pairs (pg₄, pg₅, pg₆) in the third group. The single pair of glands in the first group (fig. 20, pg₁) is visible only in cercariae dissected from snails. These glands are small, pyriform in shape, and like all the other penetration gland cells contain a conspicuous nucleus. They are situated just posterior to the eyespots, are smaller than the glands of the other groups and contain coarse granules. The ducts from these glands (fig. 20, d) are also filled with coarse granules. They first pass laterally and then dorsad to the ducts of the other groups of glands, but at the level of the mouth they turn ventrad and mesad across the other ducts and open in the concavity of the head organ median to the openings of the other ducts. The ends of these ducts and their openings can usually be seen in cercariae for a short period after the active emergence of the larvae from the snail host, but the cells themselves can no longer be seen owing to the fact that their contents have been discharged. A pair of glands such as that just described, which is present in cercariae dissected from the snail host but not in cercariae after normal emergence, has not been described by other investigators, but it seems probable that they will also be found in other

species of schistosomes. The disappearance of these glands during the normal emergence of the cercaria from the snail host suggests that their function is proteolytic, and that their contents are consumed during the migration of the cercaria through the tissues of the snail. The glands in the second group (pg₂, pg₃) are somewhat spherical in outline and are situated just anterior to the acetabulum. Their contents, as well as the contents of their ducts, are coarsely granular and stain pink with alizarin red. The ducts from these glands pass mesad and then dorsad to the ducts from the glands in the posterior group and their openings are between the openings of the ducts from the last group (fig. 19). The glands in the last group (pg₄, pg₅, pg₆) are larger, more elongated and have more finely granular contents than those in the first two groups. They are situated dorsal and posterior to the ventral sucker. Their ducts and openings are more conspicuous than those of any of the other glands (fig. 19).

At the present time there is much variation in the number of penetration glands reported for the known schistosome cercariae by different investigators. Miyairi and Suzuki (1914), Ogata (1914), and Miyagawa (1916) observed three pairs of penetration glands in the cercaria of *Schistosoma japonicum*. Leiper (1915) stated that this cercaria had five or more glands on either side. Cort (1919) and Faust (1924) reported five pairs of glands for the same species. Soparkar (1921) reported five pairs of penetration glands for the cercaria of *Schistosoma spindalis*, the two anterior pairs being distinguished from the three posterior pairs by being more granular. Faust (1919) observed three pairs of glands in the cercaria of *Schistosoma haematobium*. Manson-Bahr and Fairley (1920) and Porter (1921) confirmed Faust's observations. Bettencourt and da Silva (1922) also reported three pairs of penetration glands for *Schistosoma haematobium*, but Blacklock and Thompson (1924) observed five pairs of glands in this species and found them differentiated into two coarsely granular anterior pairs and three finely granular posterior pairs. Faust (1929) described this cercaria as having five pairs of glands, two coarsely granular anterior pairs and three finely granular posterior pairs. Iturbe (1917) observed three pairs of glands in the cercaria of *Schistosoma mansoni*. Faust (1919:166) stated that in this cercaria "the mucin glands consist of only two pairs of cells of the granular type, but, in addition, four pairs of a nongranular type, somewhat smaller and surrounding the granular cells." Manson-Bahr and Fairley (1920) and Porter (1921) also reported six pairs of glands of similar types in this species. Khalil (1922) observed five pairs of penetration

glands in the cercaria of *Schistosoma mansoni*, two anterior pairs with coarse granules and three posterior pairs with fine granules. Tanabe (1923) observed only three pairs of glands in the cercaria of *Schistosomatium pathlocopticum* and Oiso (1927) reported the same number for the cercaria of *Bilharziella yokogawai*.

The mature cercariae of five species of schistosomes, *Schistosoma japonicum*, *S. haematobium*, *S. mansoni*, *S. spindalis* and *Schistosomatium douthitti*, whose life histories have been verified by experimental work, have been reported by one or more investigators to have five pairs of penetration glands. With one exception, namely, *S. japonicum*, these glands are divisible into two anterior coarsely granular pairs and three posterior finely granular pairs. Cort (1919) observed no differentiation in the glands of *S. japonicum*. Judging from the uniformity in the number of penetration glands in the above mentioned species, it seems possible that Tanabe (1923) and Oiso (1927) may have made an error in the number of penetration glands which they reported for their species. Because data are lacking on the type of material used, it is impossible to state whether one of the six pairs of penetration glands described by Faust and others for the cercaria of *Schistosoma mansoni* is comparable with the pair which is present in the cercaria of *Schistosomatium douthitti* only before the emergence of the latter species from its snail host. While it is obvious that more careful observations are necessary before any statement of fact can be made, it seems likely that there may be a greater uniformity in the number and character of penetration glands present in different species of schistosome cercariae than has been previously suspected.

Penetration spines. A group of sharply pointed penetration spines are situated in the concavity of the head organ near the openings of the ducts from the penetration glands (fig. 19, ps). Five were always visible on each side but occasionally six were observed in each group. Whether six are always present on each side must still be determined. There are no openings in the ends of these spines nor do the spines cap the ducts from the penetration glands as practically every investigator has stated for the particular species of schistosome cercaria upon which he has worked. The contents of the penetration glands are usually extruded when a cercaria is stained intravitaly, first with Nile blue sulphate and then with alizarin red. After this treatment it can readily be seen that the extruded material is discharged through pores at the bases of the spines and not through the tips of the spines.

Digestive tract. The digestive tract consists of a long tubular esophagus which bifurcates midway between the eyespots and the

acetabulum into two short cecal pouches lying dorsal to the anterior pairs of penetration glands. The anterior end of the esophagus bends ventrad after entering the head organ and opens through a mouth situated ventrally about 0.028 mm. from the anterior end of the body. During the growth of a cercaria into an adult worm, the oral sucker is developed around the anterior part of the esophagus and the mouth in the mature worm is thus situated in the center of the sucker.

Excretory system. The excretory system of *Cercaria douthitti* consists of six pairs of flame cells, five pairs in the body and one pair in the anterior part of the tail stem (fig. 19). The first pair of flame cells lies anterior to the eyespots, the second and third pairs between the eyespots and the acetabulum, the fourth and fifth pairs between the acetabulum and the posterior end of the body. A slight variation in the position of these flame cells is always to be noticed in different individuals. There is on each side of the body an anterior collecting tubule (fig. 19, act) and a posterior collecting tubule (pct) which unite at the level of the ventral sucker into a collecting duct (cd). Each anterior and posterior collecting tubule is connected by means of capillary tubules with three flame cells. Just beyond the point of union of the collecting tubules, the collecting ducts are provided with cilia. Sometimes these cilia appear to be in two groups and may easily be mistaken for flame cells, but at other times the cilia appear to extend for some distance along the collecting ducts lateral to the ventral sucker. The two lateral collecting ducts open at the posterior end of the body into a small bladder that discharges through two ducts which surround the so-called "island of Cort." These unite shortly into a single excretory duct passing posteriorly through the tail stem. This duct divides just anterior to the forking of the tail and discharges exteriorly through a pore at the end of each tail furca.

Miller (1926) has pointed out the relation of *C. douthitti* to other known schistosome cercariae so far as the morphology of the excretory system is concerned. He placed *C. douthitti* with the cercariae of *Schistosomatum pathlopticum* and *Cercaria C* of Kemp in his group C. These three species agree in having five pairs of flame cells in the body and one pair in the anterior part of the tail stem or a flame cell pattern of $2(5 + 1)$. The cercariae of the three human schistosomes and *Cercaria Indicae* XXX of Sewell are included in his group A, all the members of which have a flame cell pattern of $2(3 + 1)$. Group B of Miller contains *Cercaria B* of Kemp, the cercaria of *Schistosoma spindalis* and *Cercaria Indicae* XLVII of Sewell. The flame cell pattern of this group is $2(4 + 1)$.

Unicellular glands. A small number of unicellular, subcuticular glands whose bodies lie in the parenchymatous tissue and are connected with the surface by a short neck are distributed over the body and tail of the cercaria. Those on the body have a more or less definite and symmetrical arrangement. These glands are made conspicuous in living cercariae by staining with gentian violet. Their distribution is shown in plate 4, figs. 26 and 27, by small circles. On the dorsal surface (fig. 26) there are two pairs at the anterior end of the body, one pair above the posterior part of the head organ, one pair a little anterior to the eyespots, one pair between the eyespots and the ventral sucker and two pairs between the acetabulum and the posterior end of the body. On the ventral surface (fig. 27) there are two pairs of glands at the anterior end of the body, a pair at the sides of the body just posterior to the attachment of the head organ to the body wall, a pair between the eyespots and the ventral sucker, a pair at the anterior edge of the ventral sucker, and a pair between the acetabulum and the posterior end of the body. The subcuticular glands on the tail have no regular arrangement. There are usually several glands scattered on the dorsal and ventral surfaces of the tail stem and a group of three or four on each surface just anterior to the forking of the tail. Several glands are always present on or near the end of each tail furca.

Brain and sense organs. The sense organs and nervous system consist of a pair of pigmented eyespots (plate 3, fig. 19, es) situated on the dorsal side between the head organ and the acetabulum, and a central nerve mass or brain (fig. 19, br), a bilobed structure situated ventral to the eyespots. The two wide lobes of the brain are connected by a narrow commissure at the level of the anterior edges of the eyespots. No nerve cords were observed.

Reproductive organs. The mass of cells posterior to the acetabulum (fig. 19, gc) is interpreted to be the primordium of the reproductive organs.

Discussion. In size and morphology *Cercaria douthitti* closely resembles the cercaria of *Schistosomatium pathlocopticum* described by Tanabe (1923). The principal difference, as already pointed out by Tanabe, is in the number of penetration glands, the former cercaria which has actively emerged from the snail host having five pairs of penetration glands and the latter three pairs. As previously stated, it seems possible that Tanabe may have made an error regarding the number of these glands present in his species.

Longevity of adults.

A few observations on rats infected with *Schistosomatium douthitti* indicate that the life of this schistosome is relatively short when compared with that of the human schistosomes. A rat infected on October 6, 1928, was killed on December 24, 1928, seventy-nine days after infection. Many male worms were recovered from both the intra- and extra-hepatic portal veins. No living females were recovered, but masses of eggs were present in the intestinal wall and liver, and many females were found in various stages of disintegration. A second rat which had been infected for a period of 136 days was killed and thirty-two male worms were removed from the liver. No female worms were present, but masses of eggs were found in the liver, indicating that females had been present although no trace of them other than the eggs were visible. A third rat, infected on October 5, 1928, was killed on September 10, 1929, or 340 days after infection. This rat apparently had received a very heavy infection and for a period of two months moved about the cage with great difficulty. During this time a few undeveloped eggs were found in the feces. There followed a period of recovery and when the rat was finally killed no trace of worms, either male or female, or eggs were found upon macroscopic examination. While more observations are necessary in order to determine the longevity of *S. douthitti* it appears that the span of life is somewhat less than one year. This is a very short period of time when compared with the longevity of the human schistosomes which is known to be twenty years or more. Christopherson (1924) reported a case of schistosomiasis haematobia in which the patient, an English physician, was known to have carried the infection for twenty-eight years.

It was impossible to obtain information on the longevity of *S. douthitti* when mice were used as hosts. The experimental mice which were not killed in order to recover the adult worms died either several days after infection because of hemorrhage of the lungs or later when enormous numbers of eggs broke through the intestinal wall causing severe hemorrhage of the intestine.

Diagnosis of genus Schistosomatium.

Generic diagnosis: Schistosomatidae. Male: forebody flattened, occupying two fifths of body; hindbody forming gynecophoric canal occupying three fifths of body; testes more than 14, at anterior end of hindbody; intestinal ceca with many lateral diverticula unite posteriorly into short cecum.

Female: body filiform, shorter than male; ovary in anterior half of body; uterus long; eggs numerous and spineless; intestinal ceca with numerous lateral diverticula unite posteriorly into a short cecum.

Cercaria: apharyngeate and furcocercous; six pairs of flame cells, $2(5 + 1)$; eyespots.

Miracidium: 2 pairs of flame cells; one pair of penetration glands; short sac-like gut; central round or oval brain.

Diagnosis of *S. douthitti*. Specific diagnosis: *Schistosomatium*. Male: length, 1.900–6.339 mm.; cirrus and cirrus pouch present; testes 15–36; genital pore ventral and on left side at anterior end of gynecophoric canal; transverse commissures joining intestinal ceca in front of cecum.

Female: length, 1.138–5.356 mm.; oötype and seminal receptacle present; transverse commissures joining intestinal ceca in front of cecum.

Cercaria: six pairs of penetration glands, first pair present only before normal emergence of larva from snail host; unicellular, subcuticular glands.

Miracidium: twenty-one ciliated epidermal cells arranged in transverse tiers; two rows of sensory cells, a posterior row terminating in bristle patches in nonciliated area between first and second tier of epidermal plates, an anterior row terminating at base of anterior papilla without bristle patches, one pair lateral nerves.

Definitive hosts: natural, *Microtus pennsylvanicus*; experimental, mice belonging to the genera *Peromyscus*, *Mus* and *Microtus*; rats belonging to genus *Rattus*.

Intermediate hosts: *Lymnaea stagnalis appressa* Say, *Lymnaea stagnalis perampla* Walker, *Lymnaea reflexa* Say, *Lymnaea palustris* Müller, *Physa ancillaria parkeri* Cuvier, *Physa gyrina elliptica* Lea.

Summary.

1. The life history of *Cercaria douthitti* has been completed experimentally in the laboratory in rats and mice.

2. The natural host of the adult worms was found to be *Microtus pennsylvanicus*. This species of mouse was trapped near ponds from which snails infected with the cercarial stage were collected.

3. Two new species of snail hosts, *Lymnaea palustris* Müller and *Physa gyrina elliptica* Lea, were discovered.

4. Every stage in the life history including adults, egg, miracidium, mother sporocyst, daughter sporocyst and cercaria was studied in detail.

5. New morphological facts discovered include a cirrus in the male; in the miracidium, a complicated sensory apparatus, definitely arranged ciliated epithelial cells, dorsal and ventral rods of cells of unknown function; in the cercaria, a pair of penetration glands present only before normal emergence of the larvae from the snail host and unicellular, subcuticular glands.

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EXPLANATION OF PLATES.

All drawings accompanied by a reference line were made with the aid of the camera lucida and details filled in at the same magnification.

Abbreviations:

act	anterior collecting tubule
ap	apical papilla
asc	anterior sensory cells
at	surface termination of anterior sensory cell
bp	bristle patch
br	brain
c	cirrus
cd	collecting duct
cgb	cercaria germ ball
cp	cirrus pouch
ct	ciliated part of collecting duct
cu	cuticle
cvt	common vitelline duct
d	duct from first pair of penetration glands
eb	excretory bladder
ep	epidermal cells
es	eyespot
esg	esophageal glands
exp	excretory pore
fc	flame cell
fn	fibrous part of brain
gba	germ ball attachment
gc	germ cell
gp	genital pore
gs	gut sac
hg	head gland
ho	head organ
j	line of attachment of head organ to body wall
lf	longitudinal muscle fibers
ln	lateral nerve
lp	lateral process
lpa	lateral papilla
m	mouth

mg	Mehlis' gland
mw	muscular wall of head organ
o	ovum
oo	oötype
os	oral sucker
ov	ovary
ovd	oviduct
pct	posterior collecting tubule
pe	primitive epithelium
pg	penetration gland
ps	penetration spine
pse	posterior sensory cells
se	subepithelial layer
sgb	sporocyst germ ball
sr	seminal receptacle
sv	seminal vesicle
t	testis
tc	transverse commissure of gut
ut	uterus
v	vitellaria
vm	vitelline membrane
vs	ventral sucker
vtc	vitelline collecting duct
ws	spineless area around ventral sucker

PLATE 1.

FIG. 1. Adult male, ventral view.

FIG. 2. Adult female, ventral view. Both male and female were drawn from stained preparations fixed after relaxation in cold water.

FIG. 3. Spines found on various parts of body of male. *A*, spines found on forebody and lateral edges of hindbody. *B*, spines found on ventral surface of hindbody. *C*, spines found on dorsal surface of hindbody.

FIG. 4. Arrangement of spines on acetabulum of male.

PLATE 2.

FIG. 5. Reproductive organs of adult female.

FIG. 6. Reproductive organs of adult male. Genital pore beneath edge of left fold of gynecophoric canal, not visible.

FIG. 7. Daughter sporocyst containing germ balls of cercariae. Removed from snail 36 days after penetration of miracidium.

FIG. 8. Mother sporocyst 17 days after penetration of miracidium, containing germ balls of daughter sporocysts.

FIG. 9. Diagrams showing arrangement of bristle patches on living miracidia. See also fig. 12.

FIG. 10. Undeveloped egg removed from uterus of female.

FIG. 11. Developed egg containing mature miracidium.

FIG. 12. Miracidium, showing arrangement of ciliated epidermal cells and relation of the sensory cells to surface and to brain.

PLATE 1.

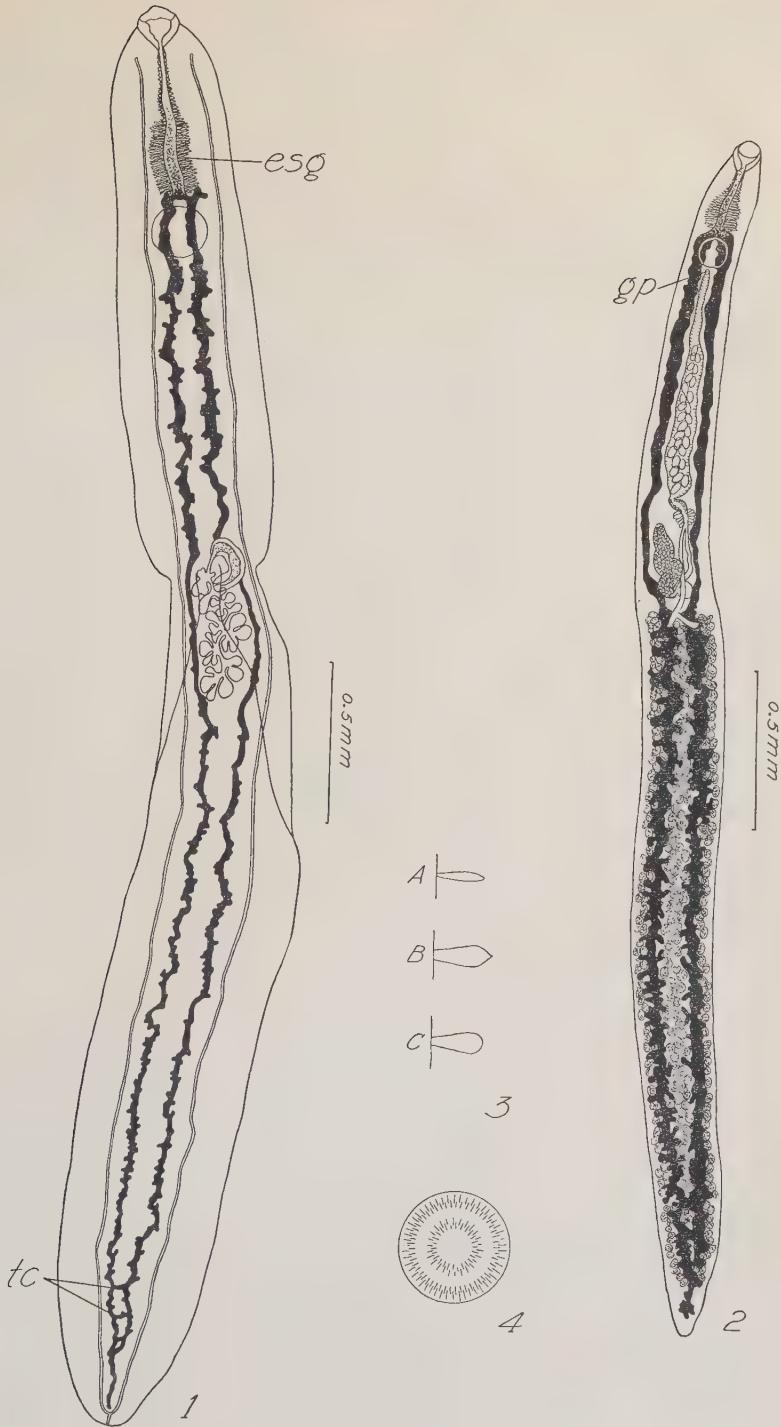


PLATE 2.

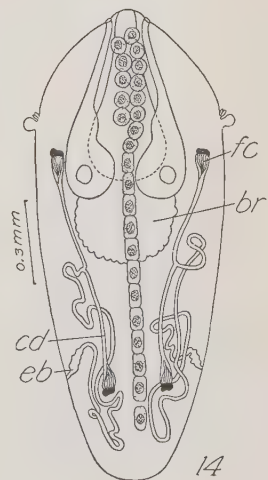
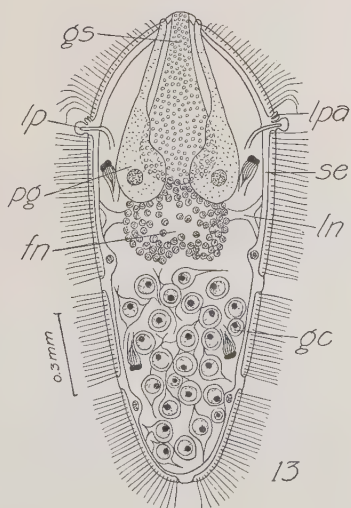
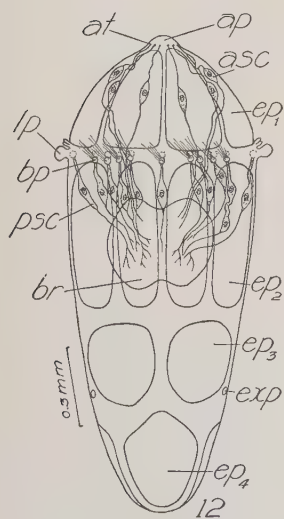
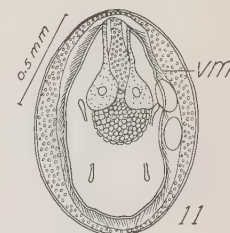
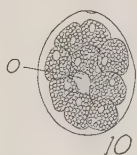
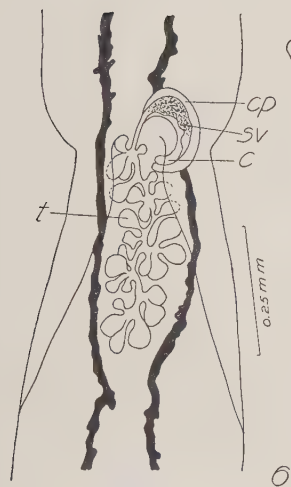
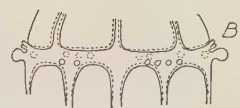
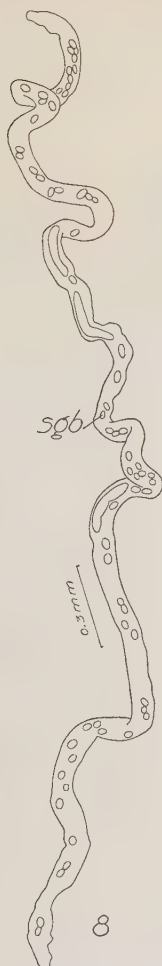
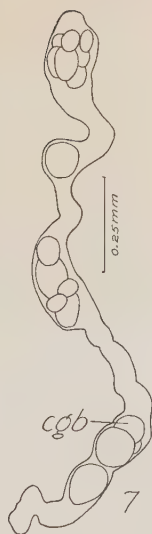
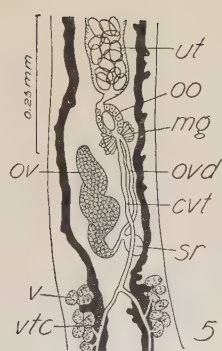


PLATE 3.

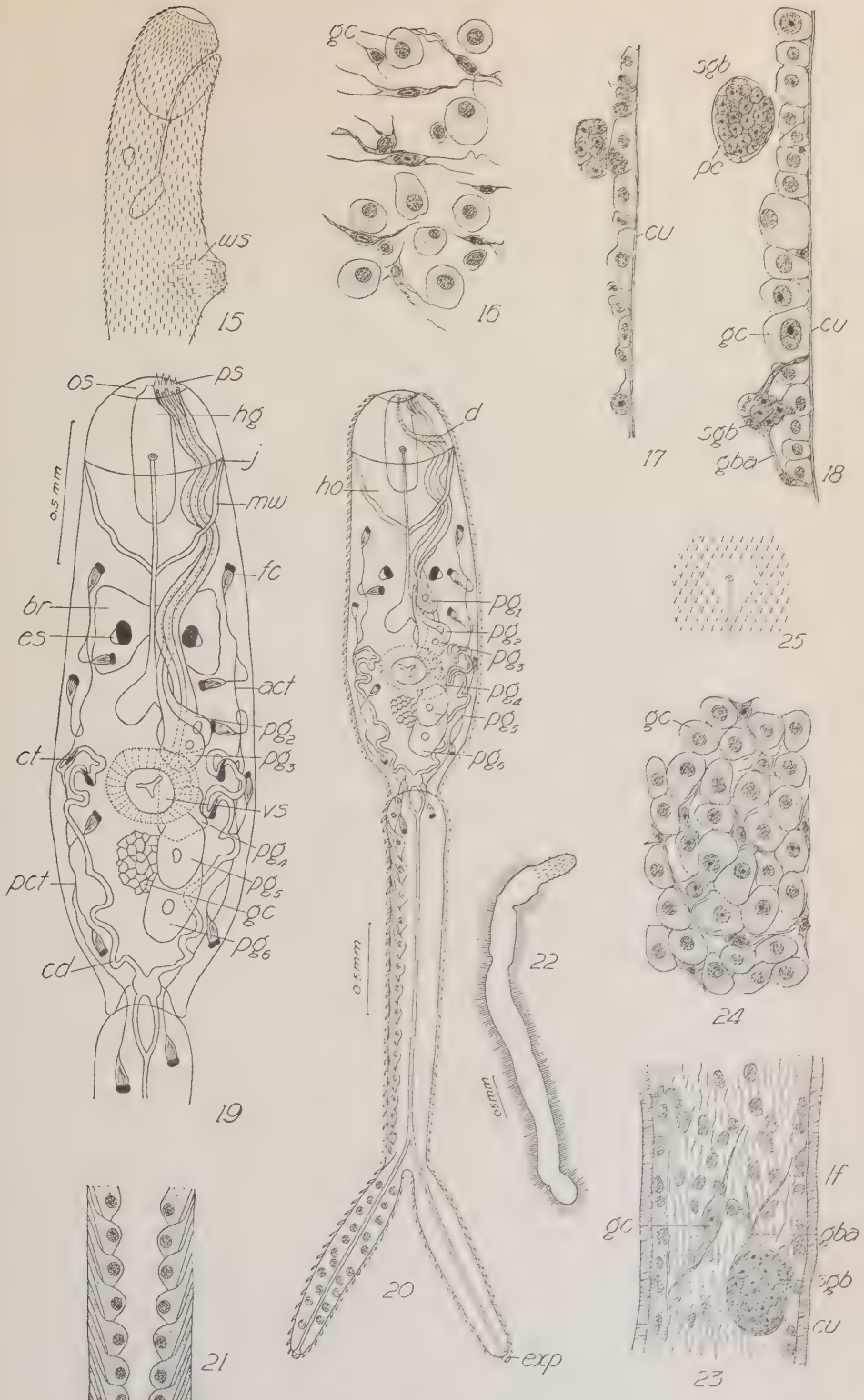
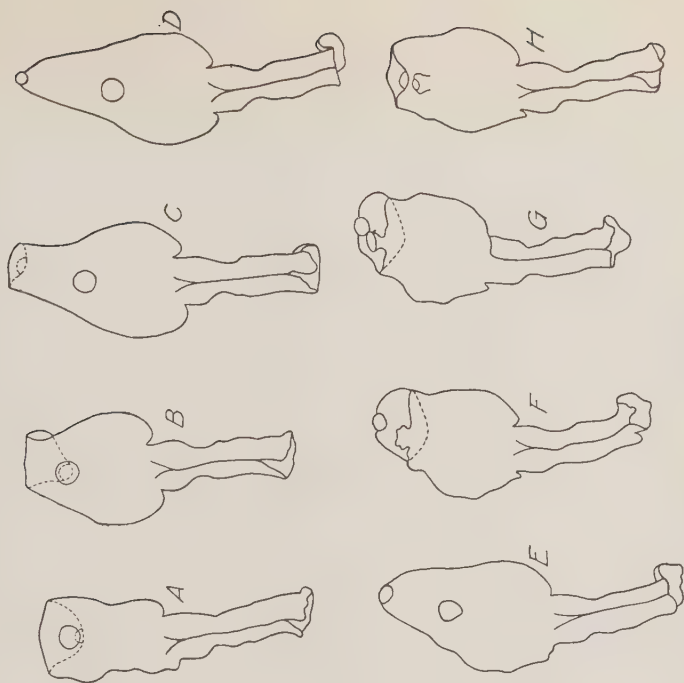
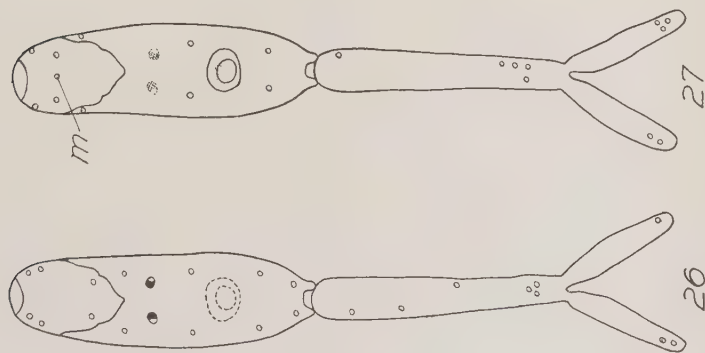


PLATE 4.



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FIG. 13. Miracidium combining optical sections at various levels and showing ciliated epidermal plates in longitudinal section, germ cells, details of brain, lateral nerves, gut and penetration glands.

FIG. 14. Miracidium with excretory system and dorsal row of cells of unknown function.

PLATE 3.

FIG. 15. Body of cercaria, side view, showing spination, position of mouth, esophagus, gut and unspined band encircling acetabulum.

FIG. 16. Surface view of daughter sporocyst showing types of cells in body wall inflated after absorption of water.

FIG. 17. Body wall of daughter sporocyst in optical section, without dilation.

FIG. 18. Body wall of young mother sporocyst in optical section.

FIG. 19. Body of naturally emerged cercaria, with details of structure.

FIG. 20. Cercaria dissected from liver of snail showing first pair of penetration glands and their ducts which disappear during the course of normal emergence. Penetration spines not included.

FIG. 21. Section of tail showing type of cells in tail stem.

FIG. 22. Young daughter sporocyst showing spines on anterior end and cilia over remainder of body.

FIG. 23. Portion of old mother sporocyst, with structural details.

FIG. 24. Body wall of young mother sporocyst in surface view.

FIG. 25. Mouth of cercaria showing circumoral spineless area.

PLATE 4.

FIG. 26. Diagram showing arrangement of subcuticular glands on dorsal side of cercaria. Drawn with aid of camera lucida.

FIG. 27. Diagram showing arrangement of subcuticular glands on ventral side of cercaria.

FIG. 28. Sketches showing movement of adult male traced from consecutive images projected from a motion picture film.

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